

Landscape resistance to dispersal: simulating long-term effects of human disturbance on a small and isolated wolf population in southwestern Manitoba, Canada

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Abstract Landscape fragmentation affects wildlife population viability, in part, through the effects it has on individual dispersal. In addition, some forms of human disturbance impinge on dispersal without physically fragmenting habitats. Here, we use the term “landscape resistance” to capture constraints to dispersal that cannot be linked directly to fragmentation. The extent to which landscape resistance can influence population persistence is not well understood. Agricultural development over the past 60 years has resulted in considerable habitat fragmentation in the Riding Mountain National Park (RMNP) region in southwestern Manitoba, Canada. We examined how

park boundaries, roads outside park boundaries and negative human attitudes have altered dispersal success and population persistence. We examined whether stochastic disturbance, representing infectious disease epidemics, further reduced long-term population persistence for various scenarios. Finally, we assessed whether the simultaneous occurrence of the three features had additive effects. We simulated dispersal using HexSim, a spatially explicit individual-based population model, parameterised with data on wolves (*Canis lupus*) in the RMNP region. Simulations that separately accounted for negative human attitudes and roads outside the park boundaries

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exhibited lower mean population size than those that ignored these details. Increasing deflection from park boundaries did not appear to have significant impacts. Our results did not indicate the presence of additive effects, and scenarios incorporating all three features had similar results as that of roads. Stochastic disturbance further reduced mean population size. Our results do illustrate how less-visible human disturbances (i.e. those that do not clearly alter landscape characteristics) can significantly limit dispersal and population persistence.

Keywords Attitudes · *Canis lupus* · Fragmentation · Population viability · Roads · Stochastic disturbance

Introduction

The mortality risks associated with dispersal are a concern for many wide-ranging species, especially those inhabiting small and isolated reserves (Soulé and Simberloff 1986; Van Vuren 1998). Human-caused barriers (e.g. fences, freeways) have reduced dispersal success in species such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) (Riley et al. 2006). The impacts can alter short-term population dynamics and may also cause longer term genetic changes. Ernest et al. (2003) attributed genetic differentiation between mountain lions (*Puma concolor*) in California's Sierra Nevada range to a combination of ecological, geographic and human-caused factors, including barriers.

The landscape matrix (areas altered by human use that surround reserves) play a critical role in connectivity because organisms frequently cross matrix lands when they disperse (Franklin 1993; Kramer-Schadt et al. 2004). We use the term “landscape resistance” to capture constraints to dispersal that, for the species under study, cannot be linked directly to fragmentation. The extent to which landscape resistance in matrix lands can influence dispersal and population persistence is not well understood. The impacts of landscape resistance will be most visible in areas where physical barriers and natural ecological discontinuities (e.g. variation in climate and elevation) are unlikely to influence animal movement.

The objective of our study was to examine how landscape resistance to dispersal can influence wildlife movement and population persistence. We hypothesised

that landscape resistance will reduce population sizes both through increased mortality and through changes in movement patterns and that these effects will be additive. Our study focused on the region surrounding Riding Mountain National Park (RMNP) in southwestern Manitoba, Canada. Agricultural development has removed forest cover up to the RMNP boundary (McNamee 1993), and RMNP is considered a wilderness island within an agricultural matrix (Carbyn 1980; Noss 1995). The behaviour of humans within this matrix affects regional wildlife population dynamics in a manner that cannot be predicted based on landscape pattern metrics alone (Brook 2008). We use a spatially explicit population model (SEPM) to link matrix characteristics to dispersal behaviour and dispersal success and to scale these individual-based impacts up to the population level.

Materials and methods

Study area

Our study area is located at the Prairie and Boreal Plain ecozone transition (Environment Canada 1993). It includes Duck Mountain Provincial Park (1,424 km²) and Forest (3,760 km²; hereafter jointly referred to as the Duck Mountains) and Riding Mountain Biosphere Reserve (15,000 km²). The biosphere reserve is comprised of 15 rural municipalities surrounding the core 2,974 km² protected RMNP (50° 46' N, 099° 59' W). The study area is part of the Manitoba Escarpment, a series of highlands (max elevation 831 masl) in western Manitoba separated by broad valleys. It encompasses numerous lakes and ponds; deciduous, boreal and mixed forest; rough fescue grasslands; and extensive marshes and wetlands (Manitoba Conservation 2004; Parks Canada 2006). Elk (*Cervus elaphus*), moose (*Alces alces*), beaver (*Castor canadensis*) and white-tailed deer (*Odocoileus virginianus*) are abundant. Other species include black bear (*Ursus americanus*), wolves (*C. lupus*), coyote, lynx (*L. canadensis*), red fox (*Vulpes vulpes*), snowshoe hare (*Lepus americanus*) and several mustelid species. Cougars (or mountain lions) are present but rare.

We examined wolves, a canid with high behavioural plasticity in food acquisition (Weaver et al. 1996) considered primarily limited by food availability

(Haight et al. 1998). Wolves are capable of dispersing several hundred kilometres in similar landscapes (Fritts 1983; Gese and Mech 1991; Wydeven et al. 1995), although human-caused mortality from intentional (trapping, hunting and predator control) and unintentional (road kill) causes is often high (Van Vuren 1998). Wolves have been present in the region for at least 5,000 years (Goulet 1993), and our study area constitutes a historically well-connected landscape for the species. An almost continuous forest corridor existed between RMNP and the Duck Mountains until the 1950s, but only 14% remained by 1991, with intense development of farmland in the centre effectively severing RMNP from other forested areas (Walker 2001).

Agriculture is now the dominant land use and occupies approximately 58% of the area (35% cropland and 23% rangeland), whereas managed public land (including parks) makes up 16% (Parks Canada 2004). Road development in the region around RMNP is extensive, with 30,000 km of roads at a density of 0.7 km of road per square kilometre (Parks Canada 2004). Wolves occupied the RMNP region until a probable combination of hunting, trapping, land clearing and poisoning caused a local extirpation around 1900 (Carbyn 1980). They recolonised RMNP by the 1930s, possibly via dispersal from the Duck Mountains (Fritts and Carbyn 1995).

Winter tracking surveys since 1976 have indicated a RMNP population of between 30 and 80 wolves (Sallows 2007), and the Park population has numbered approximately 70–75 individuals in late winter over the past 5 years. However, the high and diverse prey abundance suggests that the Park should be able to support at least 100 wolves (Keith 1983; Fuller 1989; Fuller and Murray 1998). RMNP wolves have been tracked for several multi-year studies since 1974 with no evidence of successful dispersal between the Park and surrounding areas, despite 13,000 km of ground tracking and >20 years of radio telemetry (Carbyn 1980; Paquet 1992; Stronen 2009). Mitochondrial DNA studies have identified distinct RMNP haplotypes that have not been documented outside the Park (Lehman et al. 1991; Geffen et al. 2004; Stronen et al. 2010). Microsatellite analyses also identified moderate genetic differentiation [$F_{ST}=0.053$, 95% CI 0.031–0.073] between RMNP and a genetic cluster including the Duck Mountains 30 km farther north (Stronen et al. 2011). We therefore

need a better understanding of factors that may limit wolf movement between RMNP and surrounding areas. Although no dispersal data are available, we can use modelling to explore features suspected to affect dispersal success and population persistence.

Spatially explicit population modelling using HexSim

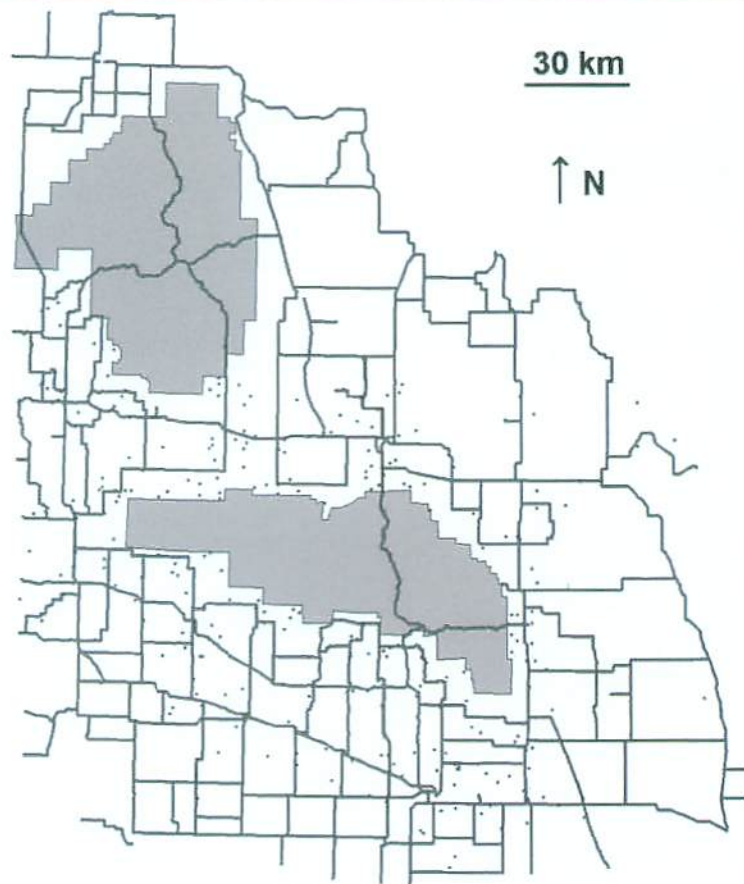
HexSim 1.3.7.1 is a SEPM suitable for modelling effective dispersal in territorial animals, where breeding requires possession of a territory. HexSim is an extension of the PATCH model (Schumaker 1998), which has been applied in over 30 peer-reviewed publications.

The HexSim model permits examination of population viability by combining spatial landscape data with information on organism response to various land cover types (Carroll 2003). GIS habitat data are assigned weights that reflect habitat quality, and survival and reproductive rates can vary based on individual access to these resources (Carroll et al. 2006; Schumaker 1998). Wolf packs (family groups) occupy habitat patches, and individual movements can take place both within and between habitat patches.

Model variables

We collected data on spatial and demographic variables believed to affect wolf dispersal and created a map of the study area (Fig. 1) using ArcView 3.3 (ESRI Inc.). Data were transferred to a raster format in ArcGIS 9.2 (ESRI Inc.) using a pixel size of 100 m. A raster calculator was then used to compute overlay of variable values. Every pixel is thus classified either as habitat, matrix, water, road or as representing hostile human behaviour. This layer was converted to a bitmap for import to our population model. Importantly, terms such as landscape and matrix may be interpreted in several ways (South et al. 2002). We refer to *landscape* as the study area (Fig. 1), *habitat* as areas supporting reproduction and *matrix* as the surrounding areas not supporting reproduction (Wiens 1997). A *patch* is a cluster of habitat pixels capable of supporting at least one breeding pair (here a wolf pack) that is separated from other such areas by matrix (South et al. 2002).

Fig. 1 The protected areas (grey colour) Duck Mountain Provincial Park and Forest (top) and Riding Mountain National Park (bottom) in southwestern Manitoba, Canada, represent areas occupied by wolves. The surrounding agricultural matrix (white colour) is not occupied by wolves. Dark grey lines represent provincial highways surrounded by 300 m buffers. Dark grey points show farms surrounded by 300 m buffers where residents responded negatively to the statement 'I enjoy seeing wolves on my land' during a mail survey on attitudes to wolves and other wildlife



Occupancy

We classified RMNP and the Duck Mountains as occupied habitat (Fig. 1). These areas have been continuously occupied by wolves for many decades (RMNP and Manitoba Conservation, unpublished data). RMNP monitoring data indicate that wolf survival in the regional agricultural matrix is dependent on the degree of local human tolerance to wolves, and shooting wolves on sight remains a common practice in the private lands adjacent to RMNP (Brook 2008). Almost the entire matrix is covered by a 1 mile \times 1 mile grid road system, which exposes animals to vehicle collision risk, as well as human hostility. Wolves at times attempt to establish territories in the matrix, but evidence from RMNP monitoring data suggest that these packs are highly vulnerable to human-caused mortality and have low persistence. We thus classified agricultural land as

unsuitable for occupancy (Carroll et al. 2006), as individuals can travel but not establish persistent territories.

Water

Wolves can disperse across large lakes during the winter months, but the popularity of such lakes for ice fishing and snowmobiling is likely to preclude such dispersal. For this reason, we considered major lakes in the matrix lands as unavailable for travel.

Roads as a measure of landscape fragmentation

The influence of roads on the movement of wide-ranging animals such as wolves is complex and depends on factors including vehicle mortality, wolf harvest management, ease of travel and human use

and attitudes, as well as the physical nature of the roads themselves (Mladenoff et al. 1995; Haight et al. 1998; Fuller et al. 2003; Whittington et al. 2005). For wolves in our study area, roads tend to increase mortality risk due to vehicle collisions and increased exposure to hostile humans. As of 2001, an estimated 10,690 km of roads were present within the biosphere reserve (Canadian Parks and Wilderness Society 2004). This is a 2% increase from 1948, and thus, most of these roads have thus been in place for over 60 years (Canadian Parks and Wilderness Society 2004).

At least one access point to RMNP exists per mile of Park boundary (Parks Canada 2004). Roads reach the edge of the Park at all these locations, but, with a few exceptions, the roads do not extend into RMNP. There is approximately 80 km of paved roads within RMNP. We included all provincial highways (both paved and unpaved surfaces) in the study area, using data from Manitoba Department of Transportation. We created a 300-m buffer around all provincial roads and consider this to represent the approximate range of an effective rifle shot from the edge of the road.

Negative human attitudes

Human tolerance to wolves in the matrix surrounding RMNP is often low (Ponech 1997; Stronen et al. 2007; Brook 2008). Although wolves are protected legally within RMNP, human-caused mortality around the Park is high (Carbyn 1980; Fritts and Carbyn 1995; RMNP, unpublished data). To simulate the influence of hostile human behaviour, we included farm locations where residents have responded negatively to the statement “I enjoy seeing wolves on my land” ($n=244$; based on effective response rate of 34%) during a mail survey on attitudes to wolves and other wildlife (Stronen et al. 2007; Brook 2008). We henceforth refer to these survey results as representing negative human attitudes towards wolves.

An unfavourable response to the above statement may not translate into actions that negatively affect wolf survival or movement (such as shooting at or chasing wolves). However, since 2001, killing of wolves in the hunting zones surrounding RMNP is illegal except in the defence of property (D. Chranowski, personal communication). Whereas it would have been possible to ask more direct questions on what action farmers would take (or would prefer to take) if they encountered wolves on their land, it is unlikely that

residents would report their farm location as well as any actions potentially considered illegal. We created 300-m buffers around Universal Transverse Mercator coordinates for farms where survey respondents disliked seeing wolves and consider this to represent the approximate effective range of a rifle shot from a farm yard.

Park boundary deflection

In parameterising our model, we predicted that the protected area boundaries would also affect dispersal. If resource competition is the principal motivation for dispersal, then individuals should move to the nearest vacant home range (Waser 1985). However, the sex-biased dispersal found in many organisms lessens inbreeding and suggests that dispersers may choose not to settle in available areas near their natal home range (Koenig et al. 1996). RMNP radio-tracking data collected weekly from fixed-wing aircraft during 2003–2006 indicate that at least five potentially dispersing wolves (as identified via exploratory movements outside their regular home ranges) continued to change their direction of travel upon encountering the RMNP boundary. Behavioural mechanisms appear to limit wolf inbreeding (Smith et al. 1997; vonHoldt et al. 2008); hence, dispersal and gene flow between RMNP and surrounding wolf populations may be vital for long-term population viability. We simulated park boundaries with varying probability of deflecting individuals that attempt to leave the park and enter the matrix in order to explore the potential consequences of dispersers changing direction when encountering the edge of a protected area and thus foregoing or delaying dispersal.

Model parameterisation

Hexagon grid

We set the width of each HexSim hexagon to 569 m. Each hexagon was 28 ha in area to allow a suitable resolution for the 300-m buffers around roads and negative human attitudes. The simulated landscape was 277 hexagons across and 295 hexagons from top to bottom.

Dispersal

We define dispersal as a movement from one territory, where the organism was born, to another territory

where it will establish and might reproduce (South et al. 2002). We use a mean dispersal of 99 (SD 116) km, based on average wolf dispersal distances in similar landscapes (Fritts and Mech 1981; Fuller 1989; Mech 1987; Gese and Mech 1991; Wydeven et al. 1995). Thus, our simulated wolves are able to disperse across 378 hexagons, maximum. The distance between RMNP and the nearest neighbouring wolf population in the Duck Mountains is 52 hexagons if travelling in a straight line.

Landscape resistance from park boundaries, roads and negative human attitudes

We explored values of 10%, 25%, 50% and 75% probability of deflection from park boundaries for individuals attempting to enter the matrix (Table 1). There was no mortality associated with dispersing into a park boundary—wolves either deflected off these edges or they moved across them into the matrix. Once in the matrix, individuals may encounter the 300-m buffers surrounding negative human attitudes and provincial highways. HexSim barriers were placed along the edges of these buffer areas and assigned probabilities for transmission, reflection and mortality. Individuals will either cross these buffers [transmission], turn back [reflection] or die [mortality]. Transmission, reflection and mortality probabilities always sum to one. We were primarily interested in exploring the effects of mortality and, for simplicity, adopted the convention that: transmission=reflection=0.5×(1−mortality). We explored values of 10%, 25%, 50% and 75% chance of mortality upon encountering roads and negative human attitudes. HexSim allows the user to set the amount of autocorrelation present in individual dispersal paths. For this study, we used a value of dispersal autocorrelation of 50%, which is midway between two biologically unlikely extremes—uncorrelated random walk and perfectly linear movement.

Population size estimates

Our population size estimates are assumed to coincide with winter, when pack size is at its minimum value for the year (Carroll 2003). RMNP performs a yearly wolf population estimate in February based on snow tracking data (RMNP monitoring data), and the monitoring records indicate an average winter population size over the past decade of approximately 70 wolves. We used a population with four stage classes

Table 1 Scenarios with varying landscape resistance to dispersal for wolves in the Riding Mountain National Park region of southwestern Manitoba, Canada

| Landscape resistance category | Scenario number | Scenario label | Properties |
|---------------------------------|-----------------|----------------|--|
| No resistance | 1 | None | Survival: max |
| | 2 | None S | Survival: 50% every 10th year |
| Negative human attitudes | 3 | A1 | Attitude mortality: 0.10 Survival: max |
| | 4 | A1S | Attitude mortality: 0.10 Survival: 50% every 10th year |
| | 5 | A2 | Attitude mortality: 0.25 Survival: max |
| | 6 | A2S | Attitude mortality: 0.25 Survival: 50% every 10th year |
| | 7 | A3 | Attitude mortality: 0.50 Survival: max |
| | 8 | A3S | Attitude mortality: 0.50 Survival: 50% every 10th year |
| | 9 | A4 | Attitude mortality: 0.75 Survival: max |
| | 10 | A4S | Attitude mortality: 0.75 Survival: 50% every 10th year |
| Deflection from park boundaries | 11 | B1 | Boundary deflection: 0.10 Survival: max |
| | 12 | B1S | Boundary deflection: 0.10 Survival: 50% every 10th year |
| | 13 | B2 | Boundary deflection: 0.25 Survival: max |
| | 14 | B2S | Boundary deflection: 0.25 Survival: 50% every 10th year |
| | 15 | B3 | Boundary deflection: 0.50 Survival: max |
| | 16 | B3S | Boundary deflection: 0.50 Survival: 50% every 10th year |
| | 17 | B4 | Boundary deflection: 0.75 Survival: max |
| | 18 | B4S | Boundary deflection: 0.75 Survival: 50% every 10th year |
| Roads | 19 | R1 | Road mortality: 0.10 Survival: max |
| | 20 | R1S | Road mortality: 0.10 Survival: 50% every 10th year |
| | 21 | R2 | Road mortality: 0.25 Survival: max |
| | 22 | R2S | Road mortality: 0.25 Survival: 50% every 10th year |
| | 23 | R3 | Road mortality: 0.50 Survival: max |
| | 24 | R3S | Road mortality: 0.50 Survival: 50% every 10th year |

Table 1 (continued)

| Landscape resistance category | Scenario number | Scenario label | Properties |
|-------------------------------|-----------------|----------------|--|
| Additive effects | 25 | R4 | Road mortality: 0.75 Survival: max |
| | 26 | R4S | Road mortality: 0.75 Survival: 50% every 10th year |
| | 27 | Z1 | Attitude mortality: 0.10 Boundary deflection: 0.10 Road mortality: 0.10 Survival: max |
| | 28 | Z1S | Attitude mortality: 0.10 Boundary deflection: 0.10 Road mortality: 0.10 Survival: 50% every 10th year |
| | 29 | Z2 | Attitude mortality: 0.25 Boundary deflection: 0.25 Road mortality: 0.25 Survival: max |
| | 30 | Z2S | Attitude mortality: 0.25 Boundary deflection: 0.25 Road mortality: 0.25 Survival: 50% every 10th year |
| | 31 | Z3 | Attitude mortality: 0.50 Boundary deflection: 0.50 Road mortality: 0.50 Survival: max |
| | 32 | Z3S | Attitude mortality: 0.50 Boundary deflection: 0.50 Road mortality: 0.50 Survival: 50% every 10th year |
| | 33 | Z4 | Attitude mortality: 0.75 Boundary deflection: 0.75 Road mortality: 0.75 Survival: max |
| | 34 | Z4S | Attitude mortality: 0.75 Boundary deflection: 0.75 Road mortality: 0.75 Survival: 50% every 10th year |

and survival and fecundity values as outlined in Carroll et al. (2006). Most wild wolves are unlikely to live longer than 4–5 years due to intraspecific strife, disease, starvation, accidents and human-caused mortality (Fuller et al. 2003), and those that do likely exhibit the survival and reproduction values we have assigned to the fourth stage class. Survival was set to 0.46 for the first stage class, 0.86 for the second, and to 0.96 for the third and fourth stage classes. Fecundity was zero for the first two stage

classes. Fecundity for the third stage class was 2.29, and for the fourth was set to 3.21.

We set maximum wolf territory size (range in HexSim) as 457 km² (Carbyn 1980). Carbyn (1980) reported RMNP mean pack size to be 8.3 wolves, and as our HexSim simulations were of females only, we set a maximum number of five females per range. Based on RMNP population surveys, and the similar size of RMNP and the Duck Mountains, we set a total population of 70 females in the study area at the start of each simulation. HexSim simulations require some time to reach a steady state, and it was the steady state results that were of interest here. Thus, all simulations were run for 500 years, but we report mean population size, number of territorial, and number of non-territorial individuals for just the final 100 years. Ten replicate simulations were averaged for each parameter combination (scenario).

Stochastic disturbance

Evidence exists that disease could play an important role in regulation of the RMNP population (Carbyn 1982). Canine distemper virus (CDV), bovine tuberculosis (*Mycobacterium bovis*) and sarcoptic mange caused by the mite *Sarcoptes scabiei* have been documented in RMNP wolves (Carbyn 1982; Stronen 2009). Local veterinarians have also recorded several cases of CDV and canine parvovirus (CPV) in dogs (*Canis lupus familiaris*) around RMNP (RMNP, unpublished data). CDV and CPV could cause high pup mortalities (Johnson et al. 1994; Mech et al. 2008), and the effects of both CDV and CPV could be significant for small and/or isolated populations (Barker and Parrish 2001). As a simple proxy for effects of infectious disease epidemics on population persistence, we added a stochastic mortality term to some of our scenarios. This additional mortality reduced the population by 50% on average every 10 years (Table 1).

Results

Population size

Simulations with increasing mortality risk owing to negative human attitudes, roads and added effects resulted in a lower mean population size than the scenario without landscape resistance to dispersal (Fig. 2a). Negative human attitudes reduced mean

Number of non-territorial wolves (floaters) in the matrix

Negative human attitudes, roads, and added effects resulted in fewer non-territorial wolves than the scenario without landscape resistance (Fig. 2c).

These “floaters” do not breed, and their survival in the matrix may have limited influence on the overall population size and number of breeders in RMNP and the Duck Mountains. Their survival in the matrix nonetheless affects gene flow between populations, and recovery time in the event that the RMNP or Duck Mountain population should be extirpated.

The number of non-territorial wolves was reduced for all scenarios with human-caused mortality, but increasing deflection from park boundaries had no effect. Stochastic disturbance combined with negative human attitudes reduced the number of non-territorial wolves by 27–57% when compared with a scenario without landscape resistance that incorporated stochastic disturbance. For simulations where stochastic disturbance was combined with roads or added effects, there were few or zero non-territorial wolves. This would increase the time needed to recolonise areas following extirpation of the local population, and the effect would be more pronounced for isolated patches at the edge of the species’ range such as RMNP. For scenarios with negative attitudes, roads and added effects (Fig. 2c), the decline in the number of non-territorial wolves was high when compared with the decline in mean population size (Fig. 2a).

Discussion

We simulated effects of landscape resistance in the form of human disturbance on dispersal and population viability. Our results indicate that increasing risk of (1) mortality or (2) a change in the direction of travel upon encountering negative human attitudes and roads could reduce population persistence in landscapes lacking obvious dispersal barriers for large mammals.

Negative human attitudes

The physical space in which negative attitudes can influence wolf mortality occupies a small portion of our simulated matrix. However, negative attitudes to wolves are likely underreported; the survey only

involved active farm operations, and many farmers did not return the survey. In addition, negative attitudes are in reality not limited to a 300-m buffer around farmyards. Examples of this situation include two wolves that died during 2005 from eating meat poisoned with insecticide (Canadian Cooperative Wildlife Health Centre, unpublished data) placed on the RMNP boundary. Wolf survival in rural agricultural areas is disproportionately influenced by the actions of people who depend on the productivity of the landscape for their livelihood (Musiani et al. 2004). In all, 51% of farmers in the RMNP region felt they had never experienced serious damage from wolves, and 44% of all farmers surveyed did not enjoy seeing wolves on their land (Stronen et al. 2007). In contrast, only 15%, 8% and 10% of farmers, respectively, disliked seeing elk, deer, and moose on their land, even though the overall value of elk and deer damage to agricultural crops exceeds losses due to wolves by a factor of at least 10–100 (Brook 2008; Gooding and Brook 2011). Furthermore, interviews with farmers indicate a marked increase in the number of elk coming out to calve in the farmlands surrounding RMNP (Brook 2008, 2010). Wolf observations reported by residents in the RMNP matrix indicated that forest cover was a better predictor of wolf occurrence than proximity to protected areas (Brook 2008). Future land clearing may therefore increase risk of human–wolf interactions and thus the mortality of wolves and other wildlife species in the RMNP region.

Deflection from park boundaries

Our simulations did not suggest that deflection from park boundaries had any effect on population persistence. Most RMNP wolf pack territories have boundaries that include the Park border, which is considered relatively marginal habitat (Carbyn 1980). It is important to consider that our simulated wolves did not learn from their encounters with humans outside the park boundaries, as real wolves are likely to do. The risk of human-caused mortality as soon as individuals cross the RMNP boundary (Fritts and Carbyn 1995) could result in locally adaptive strategies (Carbyn 1980), and individual wolves might therefore choose to seek mates within their natal population rather than enter the surrounding landscape matrix.

Roads

Increasing risk of road mortality was associated with lower mean population size and with fewer breeders and non-territorial wolves. Carnivore mortality owing to motor vehicle collisions has not been frequently reported in the RMNP region, but is a major mortality source for wolves (Callaghan 2002; Whittington et al. 2005) and grizzly bears (Benn and Herrero 2002) in other protected areas. Road mortality in the RMNP region might also be associated with animals near roads being shot from vehicles, which is likely to remain unreported. Although such mortality would be caused by negative human attitudes, it differs from mortality around farm yards in that the latter more easily can be argued to represent defence of property, which is permitted (Stronen et al. 2007). Improved human tolerance has allowed wolves to persist within higher road densities than first thought possible (Fuller et al. 2003). The high road density combined with lack of tree cover in the matrix surrounding RMNP is nevertheless likely to reduce wolf movement, particularly for individuals that have learned to associate roads, humans and vehicles with danger (Whittington et al. 2005). Even roads that do not constitute barriers (no fencing, low volume) to large mammals could therefore act as major filters to dispersal.

Stochastic disturbance

We included stochastic disturbance in the form of 50% survival every tenth year to represent infectious disease epidemics, and such disturbance had a negative effect on our simulated population. Small pre-epidemic population size is associated with elevated risk of extinction owing to infectious disease (de Castro and Bolker 2005; Gerber et al. 2005), and CPV is believed to have caused a crash in the small Isle Royale wolf population in the USA (Peterson 1995). If infectious disease epidemics were to extirpate or severely reduce small and isolated populations such as that of RMNP, the survival of non-territorial wolves in the matrix would determine the opportunity for population recovery by means of immigration from surrounding areas. Interactions between dogs and dispersing wolves are also expected to occur more often in agricultural areas, where dogs are common and often unvaccinated against infectious diseases.

Overall assessment of HexSim simulations for the RMNP region

Our results illustrate how various forms of human disturbance can reduce dispersal and population persistence, although, for many species of large mammals, they are not generally recognised as fragmenting the landscape. Such landscape resistance can occur across short distances relative to the dispersal capabilities of large mammals (Weaver et al. 1996). Further research using Global Positioning System technology could advance our understanding of features that represent landscape resistance for vagile species in human-dominated landscapes. A reserve system designed with the dispersal capabilities of a species in mind will still fail if the majority die during the attempt to move between individual elements (Van Vuren 1998). Conservation plans for the matrix surrounding protected areas must consider local human attitudes to wildlife, and negative attitudes to some species could reduce the value of otherwise suitable habitat (Brook 2008).

We were unable to examine whether negative experience with humans might influence movement decisions near roads and farms. This situation could further restrict movement in the matrix landscape for numerous species, especially those where the offspring spend several years learning from their parents prior to leaving their natal territory. Fragmentation assessments conducted strictly by examining the size and location of habitat patches may therefore overestimate landscape connectivity for small and isolated populations even for highly mobile species.

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